

First record of the stingless bee *Tetragonisca buchwaldi* (Friese, 1925) (Hymenoptera, Apidae, Meliponini) in Colombia

Jair Alonso-Alarcón¹, Diego A. Guevara², Catalina Gutiérrez-Chacón³

¹ Laboratorio de investigaciones en Abejas, Universidad Nacional de Colombia, Bogotá, Colombia

² Laboratório de Biologia Comparada e Abelhas, Universidade de São Paulo, Ribeirão Preto, Brazil

³ Wildlife Conservation Society, Cali, Colombia

Corresponding author: Jair Alonso-Alarcón (ejalonsoa@unal.edu.co)

Abstract. The stingless bee *Tetragonisca buchwaldi* (Friese, 1925) is documented in Ecuador (1925), Costa Rica (1962), and Panama (1983). This study presents new records for two provinces in Panama and the first-ever report of the species in Colombia. This last record was obtained in September 2022 in Chocó Department using pan traps, which were exposed inside the forest. These new records contribute to the general knowledge of Meliponini, mainly in the biogeographic Chocó region where these bees are under-sampled.

Key words. Apoidea, new record, taxonomy, tropical rainforest

Alonso-Alarcón J, Guevara DA, Gutiérrez-Chacón C (2024) First record of the stingless bee *Tetragonisca buchwaldi* (Friese, 1925) (Hymenoptera, Apidae, Meliponini) in Colombia. Check List 20 (5): 1286–1291. <https://doi.org/10.15560/20.5.1286>

INTRODUCTION

Stingless bees belonging to the tribe Meliponini within the family Apidae hold paramount importance within tropical ecosystems. These bees are important pollinators of native plants and crops (Heard 1999; Slaa et al. 2006; Paz et al. 2021). Their significance extends back millennia, with evidence of their use in stingless beekeeping dating back 2,000 years (Quezada-Euán 2018; Paris et al. 2020). Even today certain cultures continue to rely on these bees to procure essential products like honey, propolis, and wax (Gonzalez et al. 2018; Quezada-Euán et al. 2018).

Colombia has approximately 151 species of stingless bees (Camargo et al. 2013; Engel 2022; Ascher and Pickering 2023; Flórez et al. 2023). However, comprehensive records and taxonomic insights remain elusive for various stingless bee groups within the country (González 2007; Jaramillo et al. 2019; Guevara et al. 2020), which hamper the understanding of their distribution and impede ecological, behavioral, and conservation research efforts.

The genus *Tetragonisca* Moure, 1946 is distributed from Mexico to Argentina and encompasses four distinct species (Michener 2007; Ascher and Pickering 2023; Camargo et al. 2023). Among them, *Tetragonisca angustula* (Latreille, 1811) is the most extensively studied and used in stingless beekeeping (e.g. Nates-Parra and Rosso-Londoño 2013; Grüter 2020). This species exhibits a broad distribution across the Neotropics and potentially constitutes a species complex (Camargo et al. 2013). Conversely, *Tetragonisca buchwaldi* (Friese, 1925) is unsuited for meliponiculture due to its distinct nesting behavior in abandoned mammal burrows in the ground (Wille 1983). Its distribution remains more confined, with documented occurrences in Ecuador, Panama, and Costa Rica (Camargo et al. 2013; Ascher and Pickering 2023). While some studies delving into the biology of this species have been conducted, primarily within Costa Rica (e.g. Wille 1966, 1983; Roubik 1983, 1993; Wille et al. 1983; Sakagami et al. 1993), our new data presented here marks the first records of this species within Colombia.

METHODS

The collected material was examined in stereomicroscopy Leica MZ6. The photographs were taken using an Olympus OM-D E-m1 MARK II camera with Olympus M. ZUIKO Digital macro lens.



Academic editor: Jason Gibbs
Received: 25 April 2024
Accepted: 20 September 2024
Published: 6 November 2024

Copyright © The authors. This is an open-access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0)

To map the records of the species, we used the geographical coordinates associated with specimen labels and records of *T. buchwaldi* in the Global Biodiversity Information database (GBIF 2023a). For records that did not have exact geographical information we used Google Earth (Google, Mountain View, CA, USA) to acquire geographic coordinates. We generated maps using SimpleMappr (Shorthouse 2010). The labels of examined specimens were transcribed and added clarifying information are included by us in square brackets. The symbols: ♂, ♀ were used for worker and queen respectively.

The following institutional acronyms for repositories holding specimens examined were used: LABUN, Laboratorio de Investigación en Abejas de la Universidad Nacional de Colombia, Bogotá, Colombia (R. Ospina). RPSP, Coleção Entomológica Prof. J.M.F. Camargo, Ribeirão Preto, Brazil (E.A.B. Almeida).

RESULTS

Tribe Meliponini Lepeletier, 1836

Genus *Tetragonisca* Moure, 1946

Tetragonisca buchwaldi (Friese, 1925)

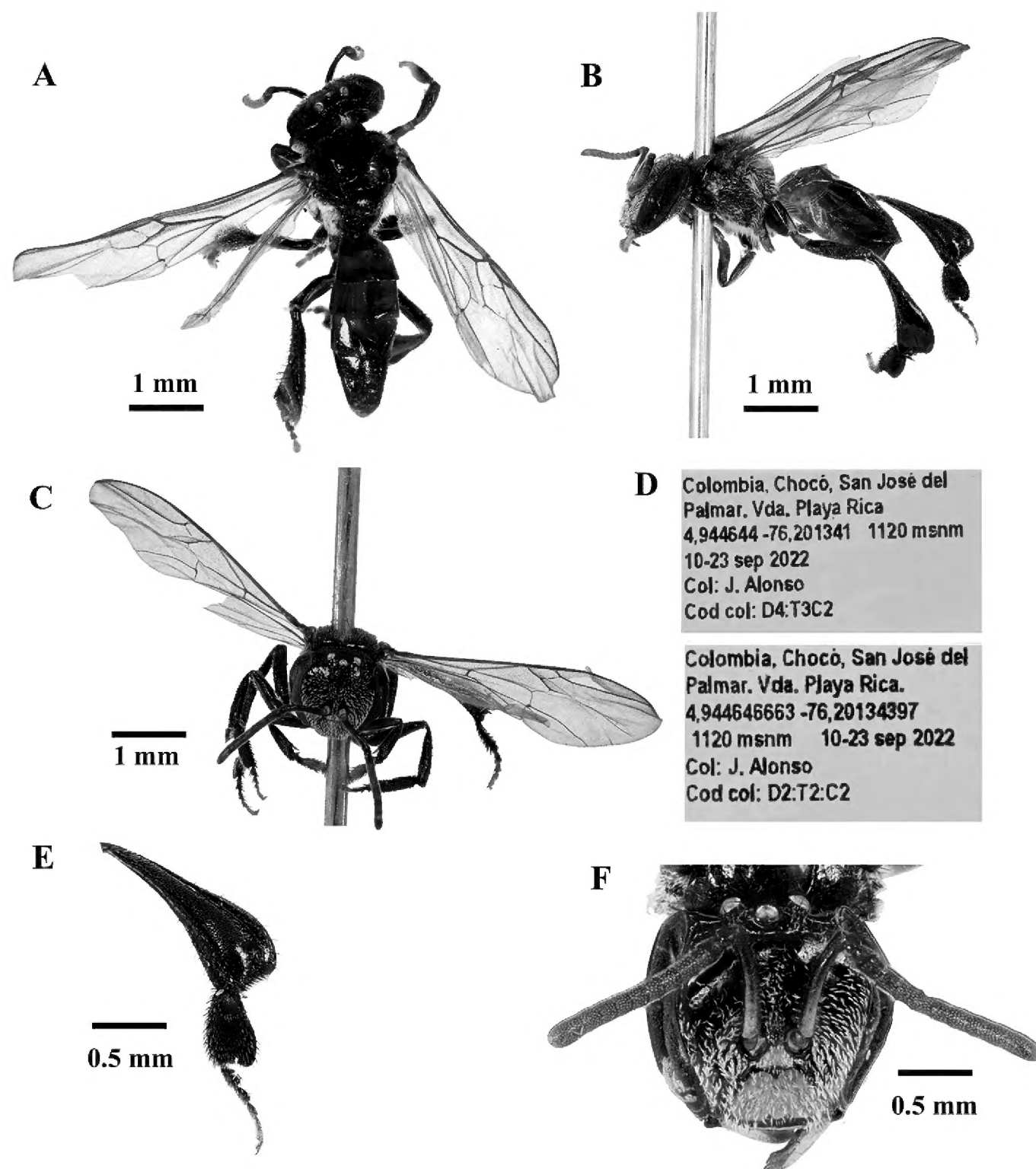
Trigona buchwaldi Friese (1925: 40 [♂, ♀]).

Figures 1, 2

New records ($n = 12$ ♀). COLOMBIA – CHOCÓ • San José del Palmar, vereda Playa Rica; 04.9446, -076.2013; 1120 m elev.; 10–23.IX.2022; J. Alonso leg., pan trap; 1 ♀, LABUN43840 • same locality; 04.9447, -076.2014; 1 ♀, LABUN4424.

PANAMA – COCLÉ • El Valle; [08.6008, -080.1303]; 585 m elev.; 13.I.1980; D. W. Inouye leg.; 1 ♀, RPSP – SAN BLAS • Res. Indígena Kuna [Kuna Indigenous Reserve]; 09.3333, -078.5000; 14–16.VIII.1985; Camargo leg.; 9 ♀, RPSP.

Figure 1. Worker of *Tetragonisca buchwaldi*. **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Frontal habitus. **D.** Collection labels. **E.** Inner surface of metatibia and metatarsus. **F.** Frontal view of head. Scale bars: A–C = 1 mm. E, F = 0.5 mm.



Other records ($n = 61$ ♀). COSTA RICA – **SAN JOSÉ** • N. de Quepos; [09.4570, -084.1387]; 30 m elev.; 2.II.1965; A. Wille leg.; 3 ♀, USP_RPSP0011480–82.

ECUADOR – **COTOPAXI** • San Francisco de las Pampas; [-0.4399, -078.9667]; 1597 m elev.; IX.1984: G. Onore leg.; 2 ♀. RPSP • same locality; 13.X.1997, S. Mateus leg; 52 ♀, RPSP 22.0517, RPSP 22.090, RPSP 22.091, RPSP 22.1284-RPSP 22.1330, USP_RPSP00011478, USP_RPSP00005195 – **PICHINCHA** • Rio Palenque, Reserva; [-0.5877, -079.3624]; 1597 m elev.; II.1983; T.M. Sharkey, L. Masner leg.; Malaise trap; 1 ♀, RPSP000035 • San Miguel de Los Bancos, 5 km E.; 0.02111, -78.84861; 1120 m elev; 29.III.1999; R. Brooks leg.; 1 sex indet., RPSP010663 RPSP.

PANAMA – **COLÓN** • Santa Rita, ridge; [09.3402, -079.7801]; 102 m elev.; 28–31.XI.1989; D. Roubik leg.; on *Bixa* [*Bixa* sp., Bixaceae]; 2 ♀, RPSP – **PANAMÁ** • Cerro Jefe; [09.2309, -079.3841]; 971 m elev.; 7.I.1980; D. Roubik leg.; 1 ♀, RPSP

Comments. We report new records of *T. buchwaldi* from the provinces of Coclé and San Blas in Panama, as well as the first report of the species from Colombia.

The specimens of *T. buchwaldi* from Colombia exhibit dark brown metasoma (Figure 1B), although the specimens from Central America and Ecuador have reddish metasoma. The two specimens from Colombia were among 442 bees collected using pan traps (one in a yellow pan and the other in a white pan).

“Suelona” probably corresponds to the common name in Cotopaxy given to these bee species for their nesting habit on the ground (“suelo” in Spanish). A sizable minority of stingless bee species exhibit this behavior (Grüter 2020).

Identification. The genus can be recognized using the keys to genera Meliponini by Silveria et al (2002), Michener (2007) and Flórez et al. (2023). *Tetragonisca* can be distinguished from other similar genera by the presence of a basal sericeous area on the inner surface of the metabasitarsus (Figure 1E) and two apical mandibular teeth (Figure 1F), unlike *Trigona* Jurine, 1807, which also present the sericeous area on the metabasitarsus and present 4–5 apical mandibular teeth. *Tetragonisca buchwaldi* differs from *T. angustula*, the only species previously reported for Colombia in this genus, by having a melanic body coloration and a slight frontal carina (light yellow body coloration, mainly in the mesosoma and frontal carina absent in *T. angustula*).

DISCUSSION

Tetragonisca buchwaldi had been previously documented in Costa Rica, Panama, and Ecuador. With these new records in Colombia, its distribution is now definitively known to encompass the entire Chocó biogeographic region, stretching from southern Panama to northern Ecuador (Figure 2). This newly recorded presence significantly contributes to our understanding of the species’ range. Furthermore, this distribution pattern is mirrored by other stingless bee species, including *Lestrimelitta galvisi* Guevara, Gonzalez & Ospina, 2020, *Nannotrigona occidentalis* Jaramillo, Ospina & Gonzalez, 2019, *Nogueirapis mirandula* (Cockerell, 1917), *Oxytrigona chocoana* Gonzalez & Roubik, 2008, *Partamona aequatoriana* Camargo, 1980, *Ptilotrigona occidentalis* (Schulz, 1904), and *Scaura argyrea* (Cockerell, 1912) (Jaramillo et al. 2019; Guevara et al. 2020; Flórez et al. 2023).

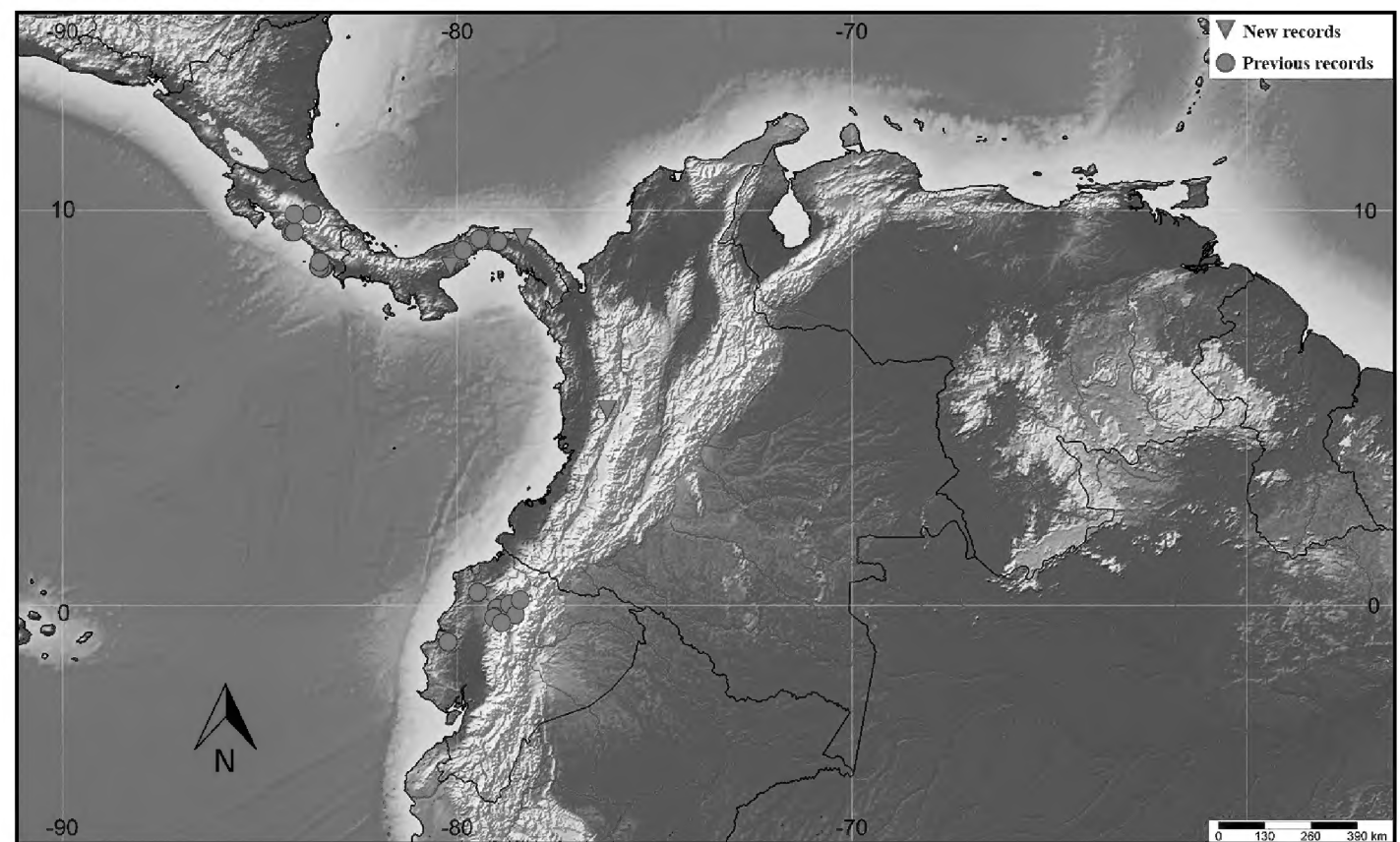
The distribution of *T. buchwaldi* appears to be closely tied to the environmental conditions unique to the lowland Pacific rainforest. The nests of this species are susceptible to melting when exposed to direct sunlight, leading to a continuous need for reconstruction. Conversely, these bees have evolved efficient adaptations for thriving within tropical rainforests, exhibiting a preference for soft, moderately shallow (15–35 cm), and well-drained soils (Wille 1966). Furthermore, their distribution may well be constrained by the biogeographical region of Chocó (de Camargo 2012).

The Colombian Pacific region remains significantly undersampled in terms of its melittofauna, leading to an underestimation of its biodiversity. This is particularly evident when considering the limited number of preserved specimens from the family Halictidae documented in GBIF (2023b). Interestingly, the Halictidae stands out as one of the most diverse and prolific families within the entirety of Colombian ecosystems (Gonzalez and Engel 2004; Smith-Pardo and Gonzalez 2007). The dearth of research groups dedicated to studying bees within this region may be closely tied to the scant information available.

The underestimated bee diversity within the Colombian biogeographic Chocó region can be attributed not only to limited sampling efforts but also to the inherent biases associated with each bee collection method employed. Sweep netting emerges as the most efficient technique, yielding a greater quantity and diversity of bee specimens, particularly in open ecosystems, although it encounters challenges in forested environments (Laroca and Orth 2002; Gutiérrez-Chacón et al. 2018). Nevertheless, this approach can be supplemented using Van Someren traps, which demonstrate effectiveness in forested settings (Smith-Pardo and Gonzalez 2007). Moreover, scent-baited traps are specialized tools for capturing orchid bees (Williams and Dodson 1971).

Additional methods such as Malaise traps and pan traps, while less proficient in capturing multitude of

Figure 2. Map with the records of *Tetragonisca buchwaldi*. New records (red triangles) and previous records (yellow circles).



species, have demonstrated their capacity to capture species that may elude other techniques (Roulston et al. 2007). Alonso-Alarcon et al. (in prep.) conducted field sampling of bees in Tatamá National Park, employing 135 color traps during 24-hour activity periods. Using this method, these authors collected 442 individuals, of which only two were *T. buchwaldi*; no other specimens of this species were captured using Van Someren tramps and entomological nets in that study. These results for the capture of *T. buchwaldi* show the low representativeness within the converted area sampled, which corresponds to the expansion zone of the Tatamá National Park.

Furthermore, we examined collections from Bogotá D.C., with over 3000 *Tetragonisca* specimens and primarily acquired using entomological nets. All of these specimens were identified as *T. angustula* or nearby morphospecies. We propose an expanded adoption of alternative collection methods, as empirical evidence suggests their combined usage serves to complement one another, providing a more comprehensive insight into the broader spectrum of bee community diversity within a given locality (Rhoades et al. 2017; Prendergast et al. 2020).

In conjunction with preceding studies (e.g. Gonzalez and Roubik 2008; Jaramillo et al. 2019; Guevara et al. 2020; Engel 2022), our new data underscore a persistent gap in our understanding of wild bees in Colombia. This knowledge deficit extends even to the corbiculate groups, which have received relatively more attention (Bonilla-Gómez and Nates-Parra 1992; Ospina-Torres and Sandino-Franco 1997; Gonzalez and Griswold 2011; Jaramillo et al. 2019; Guevara et al. 2020). The observed deficiency should catalyze heightened taxonomic investigation across various bee groups within the country. Such endeavors will facilitate the construction of a robust knowledge foundation, enabling the pursuit of studies encompassing ecology, genetics, and biogeography. Furthermore, this knowledge accumulation can pave the way for informed policy making aimed at conserving both species and terrestrial ecosystems.

ACKNOWLEDGEMENTS

We are grateful for the efforts of two anonymous reviewers who provided helpful input on the manuscript. Special thanks go to Nicolas Gutierrez for help in taking photos (Figure 1E, F.) and Steven González for editing all of these. Also, we thank the curators of the different collections, particularly Rodolfo Ospina-Torres (LABUN), Eduardo A. B. Almeida (RPSP), and Fernando Fernandez (Instituto de Ciencias Naturales - ICN) for providing access to their collections and allowing us to study the deposited material. Additionally, we extend our appreciation to the National Natural Parks of Colombia, Bezos Earth Fund, Rainforest Trust, and Andes Amazon Fund for their support in the expansion of the Tatamá National Natural Park, which allowed a new record for Colombia. This is a contribution of the Laboratorio de Investigaciones en Abejas (LABUN), Universidad Nacional de Colombia and WCS Colombia. DAG was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES), Finance Code 001 and by grant 2022-15636-7 and 2019/09215-6 Sao Paulo Research Foundation (FAPESP).

ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

Funding

DAG was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) Finance Code 001 and by grant 2022-15636-7, Sao Paulo Research Foundation (FAPESP).

Author contributions

Conceptualization: JAA. Investigation: DAG. Visualization: JAA. Writing – original draft: JJA, DAG. Writing – review and editing: CCC.

Author ORCID iDs

Emerson Jair Alonso-Alarcón  <https://orcid.org/0009-0002-6840-4506>

Diego Alexander Guevara Farías  <https://orcid.org/0000-0002-4927-6388>

Catalina Gutiérrez-Chacón  <https://orcid.org/0000-0002-8751-1035>

Data availability

All data that support the findings of this study are available in the main text.

REFERENCES

- Ascher JS, Pickering J** (2023) Bee Species Guide (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species. Accessed on: 2023-02-20.
- Bonilla-Gómez MA, Nates-Parra G** (1992) Abejas euglosinas de Colombia (Hymenoptera: Apidae) i. Claves ilustradas. *Caldasia* 17 (1): 149–172.
- Camargo JMF, Pedro SRM, Melo GAR** (2023) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region - online version. <http://www.moure.cria.org.br/catalogue>. Accessed on: 2023-08-24.
- de Camargo JMF** (2013) Historical Biogeography of the Meliponini (Hymenoptera, Apidae, Apinae) of the Neotropical Region. In: Vit P, Pedro S, Roubik D (Eds.) Pot-honey. Springer, New York, USA, 19–34.
- Engel MS** (2022) Notes on South American stingless bees of the genus *Scaptotrigona* (Hymenoptera: Apidae), part II: subgroup A of the *postica* species group. *Journal of Melittology* 110: 1–51. <https://doi.org/10.17161/jom.i110.17001>
- Flórez N, Maldonado JD, Ospina R, Ayala-Barajas R, Guevara DA, Nates-Parra G** (2023) Guía y clave ilustrada para las obreras de los géneros de abejas sociales sin aguijón (Hymenoptera: Apidae: Meliponini) de Colombia. Universidad Nacional de Colombia, Bogotá, Colombia, 52 pp.
- Friese H** (1925) Neue neotropische Bienenarten, Zugleich II. Nachtrag zur Bienenfauna von Costa Rica (Hym.). *Stettiner Entomologische Zeitung* 86 (2): 1–41.
- GBIF** (2023a) GBIF Occurrence download, taxon search: *Tetragonisca buchwaldi* (Friese, 1925). <https://doi.org/10.15468/dl.u5m9ar>. Accessed on: 2023-12-14.
- GBIF** (2023b) GBIF Occurrence download, taxon search: Halictidae Thomson, 1869. <https://doi.org/10.15468/dl.mdxy52>. Accessed on: 2023-12-14.
- González VH** (2007) Distribución geográfica de las abejas del fuego en Colombia (Hymenoptera: Apidae, meliponini, *Oxytrigona*). *Revista Colombiana de Entomología* 33 (2): 188–189. <https://doi.org/10.25100/socolen.v33i2.9342>
- Gonzalez VH, Engel MS** (2004) The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. *Entomologische Abhandlungen* 62 (1): 65–75.
- González VH, Roubik DW.** (2008) Especies nuevas y filogenia de las abejas de fuego, *Oxytrigona* (Hymenoptera: Apidae, Meliponini). *Acta Zoológica Mexicana* 24 (1): 43–71.
- Gonzalez VH. Griswold TL.** (2011) Two new species of *Paratrigona* and the male of *Paratrigona ornaticeps* (Hymenoptera, Apidae). *ZooKeys* 120: 9–25. <https://doi.org/10.3897/zookeys.120.1732>
- González VH, Amith JD, Stein TJ,** (2018) Nesting ecology and the cultural importance of stingless bees to speakers of Yoloxóchitl Mixtec, an endangered language in Guerrero, Mexico. *Apidologie* 49 (5): 625–636. <https://doi.org/10.1007/s13592-018-0590-2>
- Grüter C** (2020) Stingless bees. Springer Cham, Switzerland, 385 pp. <https://doi.org/10.1007/978-3-030-60090-7>
- Guevara DA, Gonzalez VH, Ospina, R** (2020) Stingless robber bees of the genus *Lestrimelitta* in Colombia (Hymenoptera: Apidae: Meliponini). *Caldasia* 42 (1): 17–29. <https://doi.org/10.15446/caldasia.v42n1.75511>
- Gutiérrez-Chacón C, Dormann CF, Klein AM.** (2018) Forest-edge associated bees benefit from the proportion of tropical forest regardless of its edge length. *Biological Conservation* 220: 149–160. <https://doi.org/10.1016/j.biocon.2018.02.009>
- Heard TA,** (1999) The role of stingless bees in crop pollination. *Annual Review of Entomology* 44 (1): 183–206. <https://doi.org/10.1146/annurev.ento.44.1.183>

- Jaramillo J, Ospina R, Gonzalez VH** (2019) Stingless bees of the genus *Nannotrigona* Cockerell (Hymenoptera: Apidae: Meliponini) in Colombia. *Zootaxa* 4706 (2): 349–365. <https://doi.org/10.11646/zootaxa.4706.2.8>
- Laroca S, Orth AI** (2002) Melissocoenology: historical perspective, method of sampling, and recommendations to the “Program of conservation and sustainable use of pollinators, with emphasis on bees” (ONU). In: Kevan P, Imperatriz Fonseca VL (Eds.) *Pollinating bees - the conservation link between agriculture and nature*. Ministry of Environment, Brasília, Brazil, 217–225.
- Michener C** (2007) *The bees of the world*. 2nd edition. Johns Hopkins University Press. Baltimore, USA, 953 pp. <https://doi.org/10.56021/9780801885730>
- Nates-Parra G, Rosso-Londoño J** (2013) Diversity of stingless bees (Hymenoptera: Meliponini) used in meliponiculture in Colombia. *Acta Biológica Colombiana* 18 (3): 415–426.
- Ospina-Torres R, Sandino-Franco JC** (1997) *Eulaema chocoana*, nueva especie de abeja euglosina de la costa pacífica colombiana. *Caldasia* 19 (1/2): 165–174.
- Paris EH, Castrejon VB, Walker DS, Lope CP** (2020) The origins of Maya stingless beekeeping. *Journal of Ethnobiology* 40 (3): 386–405. <https://doi.org/10.2993/0278-0771-40.3.386>
- Paz FS, De Pinto CEP, De Brito RM, Imperatriz-Fonseca VL, Giannini TC** (2021) Edible fruit plant species in the Amazon Forest rely mostly on bees and beetles as pollinators. *Journal of Economic Entomology* 114 (2): 710–722. <https://doi.org/10.1093/jee/toaa284>
- Prendergast KS, Menz MHM, Dixon KW, Bateman PW** (2020) The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* 11 (5): e03076. <https://doi.org/10.1002/ecs2.3076>
- Quezada-Euán JJG** (2018) The past, present, and future of meliponiculture in Mexico. In: Quezada-Euán JJG (Ed.) *Stingless bees of Mexico: the biology, management and conservation of an ancient heritage*. Springer, Cham, Switzerland, 243–244.
- Quezada-Euán JJG, Nates-Parra G, Maués MM, Roubik DW, Imperatriz-Fonseca VL** (2018) The economic and cultural values of stingless bees (Hymenoptera: meliponini) among ethnic groups of Tropical America. *Sociobiology* 65 (4): 534–557. <https://doi.org/10.13102/sociobiology.v65i4.3447>
- Rhoades P, Griswold T, Waits L, Bosque-Pérez NA, Kennedy CM., Eigenbrode SD** (2017) Sampling technique affects detection of habitat factors influencing wild bee communities. *Journal of Insect Conservation* 21 (4): 703–714. <https://doi.org/10.1007/s10841-017-0013-0>
- Roubik DW** (1983) Nest and colony characteristics of stingless bees from Panama (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 56 (3): 327–355.
- Roubik DW** (1993). Direct costs of forest reproduction, bee-cycling and the efficiency of pollination modes. *Journal of Biosciences* 18 (4): 537–552. <https://doi.org/10.1007/BF02703085>
- Roulston TH, Smith SA, Brewster AL** (2007) A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *Journal of the Kansas Entomological Society* 80 (2): 179–181.
- Sakagami SF, Roubik DW, Zucchi R** (1993) Ethology of the robber stingless bee, *Lestrimelitta limao* (Hymenoptera: Apidae). *Sociobiology* 21 (2): 237–277.
- Shorthouse DP** (2010) SimpleMappr, an online tool to produce publication-quality point maps. <https://www.simplemappr.net>. Accessed on: 2023-12-14.
- Silveira FA, Melo GA, Almeida EA** (2002). *Abelhas brasileiras: sistemática e identificação*. Belo Horizonte, Brazil, 254 pp.
- Slaa EJ, Chaves LAS, Malagodi-Braga KS, Hofstede FE** (2006) Stingless bees in applied pollination: practice and perspectives. *Apidologie* 37 (2): 293–315. <https://doi.org/10.1051/apido:2006022>
- Smith-Pardo A, Gonzalez VH.** (2007) Diversidad de abejas (Hymenoptera: Apoidea) en estados sucesionales del bosque húmedo tropical. *Acta Biológica Colombiana* 12 (1): 43–56.
- Wille A** (1966) Notes on two species of ground nesting stingless bees (*Trigona mirandula* and *T. buchwaldi* from the Pacific rain forest of Costa Rica. *Revista de Biología Tropical* 14 (2): 251–277. <https://doi.org/10.15517/rev.biol.trop.1966.28535>
- Wille A** (1983) Biology of the stingless bees. *Annual Review of Entomology* 28 (1): 41–64. <https://doi.org/10.1146/annurev.en.28.010183.000353>
- Wille A, Orozco E, Raabe C** (1983) Polinización del chayote *Sechium edule* (Jacq.) Swartz en Costa Rica. *Revista de Biología Tropical* 31 (1): 145–154.
- Williams NH, Dodson CH** (1972) Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution* 26 (1): 84–95. <https://doi.org/10.2307/2406985>